

REVIEW

Competitive overlap between martens *Martes americana* and *Martes caurina* and fishers *Pekania pennanti*: a rangewide perspective and synthesis

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ABSTRACT

1. Competition is a major determinant of where species occur and how species interact. Among carnivorans, interspecific competition is particularly apparent, as many of these species have evolved to be efficient killers. Theoretically, phylogenetically related carnivorans that occupy seasonal habitats, share common resources, and differ in body size by a factor of 2.5–10× should exhibit the most interference competition.
2. Fishers *Pekania pennanti* and martens *Martes americana* and *Martes caurina* are members of the subfamily Guloninae (Mustelidae, Carnivora) that occupy forests throughout northern North America. These taxa occur sympatrically throughout much of their range, utilise similar habitats, and consume similar prey; fishers and martens also differ in body size by a factor 2–5×. Consequently, these two taxa appear to be locked in particularly strong interspecific competition and should attempt to limit competitive overlap.
3. We review the current knowledge of this dyadic interaction in the framework of ecological niches and niche partitioning. In particular, we explore the three critical niche axes of diet, space, and time.
4. We found that, in contrast to the traditional view of them being highly specialised, both martens and fishers are dietary generalists; however, they also appear to be specialists in complexity, at least in space and habitats. Collectively, martens and fishers exhibit high degrees of diet and habitat niche overlap across their ranges, and this overlap is likely to have the greatest fitness consequences for the smaller and subordinate martens. Nevertheless, fine-scale habitat and prey partitioning, and especially partitioning along snow clines, seem to be the mechanisms by which these two taxa can coexist.
5. We predict that rapid ecological change – especially from increasingly homogenised forests and prey communities, as well as from declining snow cover and snowpack due to climate warming – is likely to destabilise

marten–fisher coexistence. As the climate continues to change, fishers and martens are likely to experience distributional and numerical shifts and increased isolation at their southern range boundaries, and vulnerable populations – especially of martens – will be driven to local extirpation.

INTRODUCTION

Interspecific competition is a central mechanism driving the ecology and evolution of carnivorans (Dyan & Simberloff 2005, Davies et al. 2007). Historically, the importance of competition among species of carnivores was overlooked, as bottom-up limitation of prey was considered the driver of carnivore population dynamics (Hairston et al. 1960). In recent years, however, competition has become one of the most studied biotic interactions in carnivore ecology (Davies et al. 2007, Chesson & Kuang 2008, Sévêque et al. 2020). As in all species, competition among carnivores takes form either as exploitation – where consumption of resources by one species limits the other – or as interference – where one species displaces, attacks, and sometimes kills the other. These two forms of competition are inextricably linked (Case & Gilpin 1974): a shared use of resource (exploitation) is necessary to precipitate conflict (interference). Interference competition is particularly common among carnivores because their collective phenotype is adapted to predation (Palomares & Caro 1999). Consequently, the outcomes of interspecific competition among carnivores are often dramatic, even lethal, and can limit the abundance and distribution of some carnivores (Laurenson 1995, Lindström et al. 1995, Santulli et al. 2014).

The most important factor predicting the frequency of interference competition among carnivores is body size: a carnivore that is much larger than another (i.e. $>10\times$) tends to ignore the smaller species, presumably because their resource overlap is insufficient to warrant an interaction. For carnivores that are similar in body size (i.e. $<2\times$ difference), lethal interactions are uncommon because the risk of the encounter is mutually too high for either species to initiate an attack. Pairs of carnivorans, however, that differ in body weight by a factor of 2.5–10 \times are more likely to be involved in interference competition (Donadio & Buskirk 2006), and it is most likely if the larger carnivoran is approximately four times the weight of the smaller (Prugh & Sivy 2020). In addition to body size, carnivores competing for food (Polis et al. 1989, Palomares & Caro 1999) and exhibiting dietary overlap exhibit high levels of interference competition (Schaller 1972, Mills & Biggs 1993). Such competition and conflict are heightened in seasonal environments that feature periods of resource and prey deficits (Palomares & Caro

1999). These effects are particularly pronounced among the more predatory (as opposed to scavenging) carnivorans, which have the anatomy and behaviours to engage more in direct interference competition (Donadio & Buskirk 2006). Finally, evolutionary relatedness influences antagonistic interactions, as carnivores generally interact more with species in the same family (Donadio & Buskirk 2006). All of this assumes, of course, that competing carnivores are in the same place at the same time.

Fundamental to competition is a species' niche – the environmental conditions enabling population stability (Hutchinson 1957, Holt 2009) – and the ability of sympatric species to partition (Hardin 1960) the critical niche axes of space, time, and resources (Schoener 1974). Among competing carnivores, modification of space use (Fedriani et al. 2000, Berger & Gese 2007), diel activity (Cusack et al. 2017, Dröge et al. 2017, Frey et al. 2017), and resource consumption (Crooks & Van Vuren 1995, Karanth & Sunquist 1995) to limit competitive overlap is common. Moreover, because the interactions are often asymmetric and based on body size, the smaller and typically subordinate species often alter their realised niches accordingly through adaptive foraging (Harrington et al. 2009), habitat selection (St-Pierre et al. 2006), or activity patterns (Bischof et al. 2014). Changes in realised niches that limit competition, though, can also lead to indirect fitness consequences, alter species' distributions (King & Moors 1979), or influence evolutionary trajectories (e.g. character displacement) that enable structured use of space and resources among different-sized carnivores (Davies et al. 2007). Historically, research has focused on one or two of the critical niche axes, but increasingly research is exploring changes among all niche axes concurrently to improve our understanding of carnivore communities and interactions (e.g. Rodriguez Curras et al. in press).

Based on first principles, fishers *Pekania pennanti* and the martens *Martes* spp. found in North America should exhibit pronounced interspecific competition: they differ in body size by a factor of 2–5 \times ; exhibit high degrees of spatiotemporal and dietary overlap in strongly seasonal environments; are both highly predaceous carnivores; have a shared evolutionary history, occurring within the same subfamily (Guloninae); and generally occupy the same places and habitats. Indeed, martens and fishers exhibit considerable overlap in their ranges such that the geographical range of fishers is almost completely nested within

the range of martens (Fig. 1). Martens occur further north, to the northern limit of trees and, in the Rocky Mountains, further south into New Mexico. In addition to being phylogenetically related (fishers and martens diverged 9–13 million years ago; Law et al. 2018) and having distributional overlap, martens (0.5–1.5 kg) and fishers (2–5.5 kg) possess similar body sizes and diets (especially small mammals), both are forest carnivores, and are commonly found in syntopy. Fishers and martens are direct competitors and exhibit strong competitive interactions, with particularly notable consequences for the smaller and subordinate species: the martens. Indeed, interference interactions between martens and fishers have been noted since the early 1900s (Hardy 1907, Grinnell et al. 1937), and trapping records have consistently shown an inverse relationship in the relative abundances of these species at regional and landscape scales (Strickland & Douglas 1987, Jensen & Humphries 2019, Suffice et al. 2020). Yet, these two taxa have coexisted over millennia. This stable sympatry has been of interest to ecologists for decades (e.g. Rosenzweig

1966), yet research on mechanisms of coexistence has emerged only recently.

We explore the role of competition in defining these taxa and the niche axes that these taxa partition – specifically differential habitat selection and divergent diets, spatial segregation, and temporal avoidance – to allow their coexistence. While two species of martens inhabit North America – American martens *Martes americana* and Pacific martens *Martes caurina* – our review focuses on the interaction of martens (i.e. both representatives of the genus *Martes* that occur in North America) with fishers. We took this approach as these two close relatives diverged recently, during the late Quaternary period (Stone & Cook 2002), and were historically considered conspecifics (but different subspecies) based on morphological data (Wright 1953, Clark et al. 1987). More recently, these *Martes* taxa were revised into specific status via molecular approaches (Stone & Cook 2002). In the few places where American and Pacific martens are in contact, they have been shown to hybridise (Colella et al. 2019), which has even led to

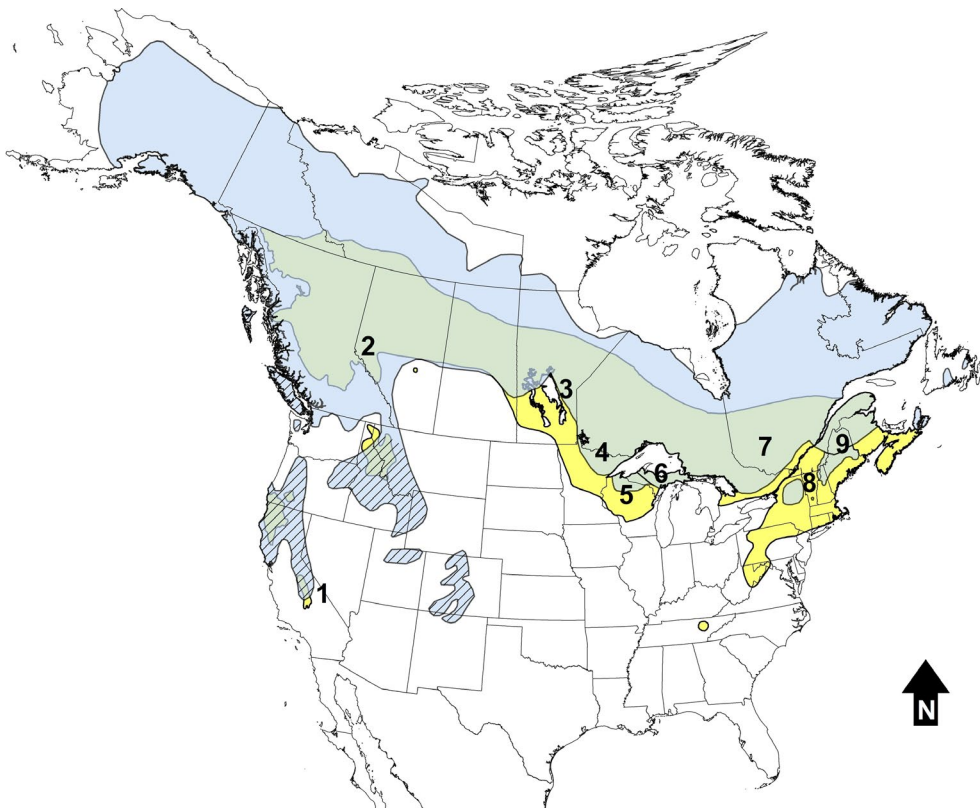


Fig. 1. Geographical ranges of martens *Martes americana* and *Martes caurina* and fishers *Pekania pennanti* in North America. Blue fill represents areas where martens occur without fishers (hatched lines represent overlap between *Martes americana* and *Martes caurina*); yellow fill for where fishers occur without martens; green is regions of sympatry, where both species occur. Also provided are numbered locations of reviewed papers that explored marten and fisher niche overlap in: 1) California, USA (Zielinski et al. 2017); 2) Alberta, Canada (Fisher et al. 2013); 3) Manitoba, Canada (Raine 1972); 4) Minnesota, USA (Manlick et al. 2020); 5) Wisconsin, USA (Manlick et al. 2017b, 2020, McCann et al. 2017); 6) Michigan, USA (Croose et al. 2019); 7) Quebec, Canada (Suffice et al. 2020); 8) New York, USA (Jensen & Humphries 2019); and 9) Maine, USA (Krohn et al. 1995).

uncertainty around which species of marten occur at a few locations (Pauli et al. 2015, Grauer et al. 2017). Consequently, both species share a number of similarities in body size, habitat associations (Thompson et al. 2012), foraging ecology (Manlick et al. 2019), and life-history characteristics (Pauli et al. 2012). The differentiation between the two *Martes* spp. appears to be slight, especially when considering their competition with fishers. Finally, by combining these two similar congeners we are able to leverage the full complement of literature to understand their strong competitive interaction with fishers. Nevertheless, comparing studies can be difficult due to different spatial scales of inquiry that range from local (<500 km²) to regional (>30000 km²), divergent data types and methods, and different model covariates considered. Moreover, investigations into marten–fisher interactions and co-occurrence have been conducted in different regions of sympatry and allopatry where abiotic and biotic contexts differ markedly (Fig. 1). Even with those caveats, marten and fisher interactions have been extensively studied, providing a unique opportunity to review this dyadic competitive interaction and elucidate some emergent patterns that are consistent across spatiotemporal scales not only for these two taxa but also for carnivores in general.

METHODS

We searched Web of Science and Google Scholar, using terms including marten, fisher, *Martes*, *Pekania*, competition, predation, space, time, habitat, snow, diet, and prey. To broaden our search, we also used a ‘snowball’ method, in which we reviewed the references of all included papers, and used the search engines to identify papers that cited included papers. We reviewed papers for information on competition between martens and fishers and the niche axes that these taxa partition.

RESULTS AND DISCUSSION

Diet partitioning and overlap

Throughout their ranges, martens and fishers are dietary generalists that forage on a diverse suite of prey ranging from arthropods (e.g. Hymenoptera) and seed mast to snowshoe hares *Lepus americanus* and vertebrate carrion. Both taxa also exhibit substantial dietary plasticity, readily adapting their diets across seasons and years.

Both species of martens in North America – *Martes americana* and *Martes caurina* – display widespread generalism; nevertheless, small mammals constitute staple prey throughout their ranges. Arvicolid rodents (e.g. voles, lemmings) in particular are the most important prey item for martens in many ecosystems. Indeed, voles (*Microtus*

and *Myodes* spp.) comprised at least 25% of marten diets in systems ranging from New Brunswick, Canada (Cumberland et al. 2001), to the central Rocky Mountains (Gordon 1986), Sierra Nevada, USA (Zielinski et al. 1983, Hargis & McCullough 1984), and coastal Alaska, USA (Flynn et al. 2005). In the extreme, arvicolid rodents comprised nearly 90% of the diet of martens from central Alaska (Buskirk & Macdonald 1984). Numerous studies have also documented strong correlations between marten abundance and the availability of arvicolid prey (Weckwerth & Hawley 1962, Thompson & Colgan 1987, Flynn & Schumacher 2009), and the low abundance of this key prey group has been cited as a potential limitation to marten recovery efforts (Carlson et al. 2014).

Nevertheless, martens also readily exhibit prey switching in the absence of preferred prey. Ben-David et al. (1997) demonstrated this foraging plasticity over four years in Alaska, where martens not only selected for small rodent prey (17–45% of diet) but also readily consumed berries (13–31%), birds (30–47%), carrion (26–32%), salmon *Oncorhynchus* sp. (7–29%), and red squirrels *Tamiasciurus hudsonicus* (15–35%). This dietary plasticity is consistent with observations of prey switching and dietary generalism apparent across western marten populations. For example, coastal martens across the Pacific Northwest exhibited widespread use of berries, marine-derived prey (e.g. salmon, intertidal invertebrates), and terrestrial vertebrates (Manlick et al. 2019), including large proportions of avian prey (Nagorsen et al. 1989, 1991). Martens in coastal California and Sierra Nevada, USA, also exhibit considerable prey switching between seasons and consume high proportions of avian, herptile, and insect prey relative to other regions, likely due to the absence of more profitable prey such as snowshoe hares (Zielinski et al. 1983, Zielinski & Duncan 2004, Slauson & Zielinski 2017). Indeed, most instances of prey switching appear to be driven by the absence of preferred prey (e.g. Ben-David et al. 1997). Thompson and Colgan (1987, 1990) found that martens in Ontario, Canada, significantly increased dietary breadth in the absence of arvicolid rodents, switching to less preferred prey such as shrews *Sorex cinereus*, ruffed grouse *Bonasa umbellus*, and red squirrels. However, prey switching was also tied to numerous demographic consequences, including reduced population densities and ovulation rates, limited reproduction, expanded home ranges, and even cannibalism (Thompson & Colgan 1987).

In contrast, fishers are often considered porcupine *Erethizon dorsatum* specialists (Powell 1981, Martin 1994) that are capable of regulating porcupine populations (Pokallus & Pauli 2015), but fishers actually exhibit widespread dietary plasticity throughout North America (LaPoint et al. 2015). For instance, Arthur et al. (1989) found that fishers in Maine, USA, not only consumed

porcupines (14%) during winter months but also took considerably larger proportions of fruit (37%), squirrels (25%), and small mammal prey (e.g. shrews, voles; 22%), while other populations exhibit minimal consumption of porcupines even in the absence of other preferred prey (<1%; Kuehn 1989). In New York, USA, fishers primarily consumed white-tailed deer *Odocoileus virginianus* carrion and snowshoe hares in winter (Brown & Will 1979). In Wisconsin, USA, small mammals and porcupines constituted the largest portions of fishers' diets (63%; Kirby et al. 2018). In Washington, USA, fishers primarily consumed mid-sized mammalian prey such as snowshoe hares and mountain beavers *Aplodontia rufa* (Parsons et al. 2020). Collectively, fishers are generalist foragers and rely on large mammalian prey such as squirrels, snowshoe hares, and deer carrion (*Odocoileus* spp.) that provide large amounts of metabolisable energy (Powell 1979, Golightly et al. 2006, LaPoint et al. 2015). Notably, the Endangered Pacific fisher subpopulation in the southern Sierra Nevada of California exhibits significant differences in diet from other regions of the country. Similar to regional marten populations, these fishers consume much higher proportions of avian, herptile, and insect prey and fungi compared with those in other regions (Zielinski et al. 1999, Golightly et al. 2006, Smith et al. 2021), and consume significantly lower proportions of larger prey such as deer and snowshoe hares (LaPoint et al. 2015). Prey switching in the absence of preferred resources has also been noted in fisher populations (Kuehn 1989, Bowman et al. 2006, Golightly et al. 2006), as have seasonal and temporal diet shifts (Giuliano et al. 1989, Zielinski et al. 1999).

The observed dietary preferences ostensibly support the hypothesis that differences in dietary specialisation based on body size enable coexistence (Rosenzweig 1966): martens specialise on arvicolid rodents, and fishers take larger rodents and lagomorphs. Given the high degree of generalisation and prey switching, however, dietary overlap is also common, especially in winter months when prey is limiting. For example, Raine (1987) documented the extensive use of snowshoe hares by both martens (59% of scats) and fishers (84%) in Manitoba, Canada, while Clem (1977) observed greater dietary overlap between martens and fishers in winter than in summer. Manlick et al. (2017a,b) and Zielinski and Duncan (2004) also observed near-complete dietary overlap between martens and fishers in Wisconsin and California, respectively. Nevertheless, dietary overlap is likely to have significant consequences for the subordinate competitors, martens. Raine (1987) documented marten remains in 5% of fisher scats during a period of high dietary overlap, while Weir et al. (2005) detected marten remains in >10% of fisher stomachs. In Wisconsin, fishers are the primary cause of winter mortality in martens (McCann et al. 2010), probably due to

high dietary overlap and limited niche partitioning, and fishers have been implicated in the delayed recovery of reintroduced martens (Manlick et al. 2017a,b).

Spatial partitioning and overlap

FOREST AND LAND COVER

Several studies and reviews (Buskirk & Powell 1994, Raley et al. 2012, Thompson et al. 2012, Gilbert et al. 2017) have focused on habitat use and selection of martens and fishers; while regional differences across North America occur, some common patterns have emerged. Although martens and fishers were previously reported to require mature coniferous forests (Buskirk & Powell 1994), research has documented a diverse use of forest types, including coniferous, mixed, and deciduous-dominated stands (Katnik 1992, Payer & Harrison 1999, Wright 1999, Dumyah et al. 2007, Raley et al. 2012). Chapin et al. (1997) investigated stand-scale selection by martens in a forest reserve in Maine and failed to detect differences in selection indices during summer or winter among mature (>12 m height) and well-stocked (>50% canopy closure) stands of deciduous, coniferous, and mixed forests. In general, research has demonstrated that marten and fisher use of specific habitats is related to structural attributes of forest stands (e.g. complex vertical and horizontal structure provided by a closed-canopy, coarse woody debris, snags, stand age, and tree cavities) rather than to any particular overstorey species composition. A complex structure enables both taxa to meet life-history requirements for denning, kit rearing, foraging, thermoregulation, resting, and escaping predators (Buskirk & Powell 1994). Payer and Harrison (2004) investigated the relationship between the intensity of habitat use by martens and forest structure in Maine and concluded that martens can occupy a wide range of forest stand types and ages where complex structure is abundant. The authors indicated that differences in stand-scale selection reported in the literature may reflect common within-stand habitat attributes, suggesting that forest composition and stand age, which varies regionally, may be surrogates for the complex structure required by martens. Given their dependency on complex forest structure, it is not surprising that both taxa largely avoid open areas and areas with recent timber harvests.

The influence of other anthropogenic land uses and disturbance on martens and fishers varies. Martens appear to be more sensitive to disturbance than fishers (Fisher et al. 2013); however, the influence of roads on fishers has varied among studies (Fuller et al. 2016, Manlick et al. 2020). Furthermore, fishers now occupy much of their historical range in eastern North America, which is a heterogeneous landscape of agriculture, forest, and urban

development. LaPoint (2013) documented fisher habitat use within a suburban landscape, where he observed behavioural adjustments in timing of activity and high use of corridors linking forest patches, which he hypothesised enhanced survival and facilitated movements. Stewart et al. (2019) examined fisher resource selection and movement in a human-altered landscape and observed selection for anthropogenic patches connected by forested corridors; moreover, large-scale genetic analysis showed fisher distribution across the heavily developed Alberta, Canada, landscape was panmictic, rather than fragmented (Stewart et al. 2017). Overall, these patterns suggest that fishers are less sensitive to human disturbance than martens and exhibit more plasticity in habitat selection.

While our understanding of marten and fisher habitat use and selection at several spatial scales has advanced in the past several decades, more recent work has focused on understanding the underlying drivers of species' occurrence where populations are sympatric and testing competing hypotheses representing different coexistence mechanisms, including habitat partitioning. The spatial scale of these studies has varied considerably; however, most have been conducted at landscape and regional scales and involved the use of non-invasive surveys as opposed to the radiocollared animals that have commonly been used for investigating habitat selection.

Fisher et al. (2013) found evidence for habitat partitioning in the mountains of west-central Alberta, where martens occurred in more coniferous forest with less mixed forest, and fishers used landscapes with less dense coniferous forests, less open wetlands, and more shrub cover. Additionally, martens were negatively associated with habitat fragmentation caused by oil exploration via seismic lines, whereas fishers showed no response to this disturbance. Results of the remaining studies reviewed here, all at the southern extent of the marten and fisher range, did not support habitat partitioning. In the Sierra Nevada, Zielinski et al. (2017) found a high degree of overlap between habitat types used by both taxa and reported that abiotic drivers (i.e. snowpack, precipitation, and temperature) were most influential for explaining patterns in occurrence. Similarly, in the north-eastern USA, both martens and fishers selected for coniferous forest, and abiotic conditions (and presumably productivity) mediated intraguild interactions (Jensen & Humphries 2019). Lastly, three studies in the upper Great Lakes region failed to support habitat partitioning as a coexistence mechanism: marten and fisher selected similar forest cover types in Michigan, USA (both positively related to deciduous stands; Croose et al. 2019), and Manlick et al. (2017a,b), Manlick et al. (2020) found no clear patterns of habitat partitioning in their study areas in Wisconsin and Minnesota, USA.

Collectively, a high degree of overlap in marten and fisher habitat use reported in the literature highlights a

lack of support for habitat partitioning as a mechanism of coexistence south of the boreal forest. These results are not surprising, given the degree of dietary overlap noted above. However, we acknowledge that our understanding of habitat partitioning, particularly at fine scales, is incomplete due to the lack of studies that have concurrently estimated space use and resource selection of co-occurring martens and fishers. Zielinski et al. (2017) reported space use (but not resource selection) of martens and fishers and indicated that interspecific home range overlap was common and occurred in 71% of marten home ranges and in 15% of fisher home ranges. In northern Wisconsin, areas of interspecific overlap ranged from 50 to 100% of home range areas (Wright 1999); however, similar to Zielinski et al. (2017), this work was limited to estimating home range boundaries and not utilisation distributions, which would more fully elucidate overlap in space use (Fieberg & Kochanny 2005).

ABIOTIC FACTORS

Snow has long been considered a primary abiotic factor influencing marten and fisher sympatry. Larger fishers possess higher foot loads and sink into snow more than the smaller martens with smaller foot loads that can 'surf' the snow (Raine 1983), suggesting an important additive energetic cost to fisher movement across snowy landscapes. Additionally, martens are adapted to foraging within the subnivium (*sensu* Pauli et al. 2013), conferring a competitive advantage to martens (Raine 1983, Buskirk & Powell 1994) in deep snow by providing exclusive access to small mammal prey during the winter. This advantage over fishers may be especially significant in areas where a deep snowpack coincides with low-productivity conditions, where larger-bodied prey are less abundant (Jensen & Humphries 2019).

Using trapping records from Maine, Krohn et al. (1995) found support for their hypothesis that frequent and deep snow limits fishers but not martens. Local spatial partitioning could be explained by snowfall frequency (and inferred accumulation), although the authors did not explicitly consider alternative hypotheses, such as other abiotic conditions and the influence of forest canopy density in creating variation in snow depth. Krohn (2012) conducted a subsequent analysis of historical fur harvests for martens and fishers across the continent, and found that shifts in distribution over the last century fit with expectations from changing continental patterns of snowfall. The author also acknowledged that other factors – anthropogenic disturbance, unregulated trapping, etc. – are likely to have contributed due to substantial observed variability. One potential source of variability is the interaction between forest structure and snow, an effect that has been found

to be not only strong but also complex and highly variable (Varhola et al. 2010). The forest canopy intercepts snowfall, resulting in shallower snow under the canopy, but can also influence wind and solar radiation, which causes snow melt or retention. However, the magnitude of these effects varies by canopy density and forest type (deciduous vs. coniferous) and latitude (influencing solar angle and temperature), as well as topographic characteristics such as slope and aspect (Petty et al. 2015, Thompson et al. 2018). How these interactions influence fisher and marten niche dynamics is not well understood, but they are likely to contribute to the substantial regional variation that has been observed in the co-occurrence of these two taxa. Regional empirical studies have examined the spatial dynamics of fishers and martens, and four studies have identified snow and elevation as the most influential predictors for understanding differences in marten and fisher distributions and co-occurrence (Manlick et al. 2017b, 2020, Zielinski et al. 2017, Jensen & Humphries 2019).

In southern Sierra Nevada, Zielinski et al. (2017) found threshold relationships between climate and fisher and marten presence. Fishers were never detected in areas with a deep April 1 snowpack (>650 mm), and martens were not detected in drier and warmer areas. However, in the driest area – a high-elevation plateau – only fishers were detected, indicating that, in the absence of deep snow and other limiting abiotic conditions, fishers can exploit atypical high-elevation habitat types usually associated with martens. In the Adirondack Mountains of the north-eastern USA, there was a strong positive relationship between fisher occurrence and late winter minimum temperature (Jensen & Humphries 2019). At lower elevations where temperatures were warmer, the relative abundance of fisher populations increased and, in combination with more abundant coyote *Canis latrans* populations, presumably excluded martens through interspecific killing or intraguild predation (Jensen & Humphries 2019). In the central Adirondack Mountains where elevations were higher, lower temperatures combined with low-productivity and deep snowpack limited fishers and facilitated their coexistence with martens. Preliminary results of additional research in this study area using camera traps and multispecies occupancy models also suggest that co-occurrence of martens and fishers appears to be primarily mediated by winter abiotic conditions, specifically temperature (P Jensen, unpublished data).

The influence of deep snow on fisher and marten spatial partitioning has been shown to vary regionally and can be dependent on interactions between both abiotic factors (e.g. snow depth, density, and persistence) and biotic factors that mediate differential competitive advantages. For example, Jensen and Humphries (2019) hypothesised that deep snowpack is not spatially limiting to fishers if larger

above-snow (supranivia) prey resources are sufficient; however, in low-productivity environments featuring deep snowpack martens hold the competitive advantage, and fishers (larger, but poorer competitors) persist because of increased intraguild predation. Manlick et al. (2017a,b) similarly proposed intraguild competition as the mechanism of coexistence in northern Wisconsin, where marten occupancy was consistently low and spatial, temporal, and dietary partitioning with fishers was non-existent. Moreover, Manlick et al. (2017a,b) and Manlick et al. (2020) found a consistent, negative effect of snow on fishers in both Wisconsin and Minnesota and hypothesised that increasing human impacts (e.g. from roads) and snow compaction from warming winter temperatures will facilitate fisher movement in future.

Varying conclusions about the importance of snow are likely to be partly due to scale dependency. Spatial partitioning is most likely to occur at regional scales, due to the corresponding scales at which abiotic and biotic factors vary (Amarasekare 2003) and alter the competitive ranking of coexisting species. Thus, research conducted at local scales may not detect heterogeneity that is present at larger spatial scales. This may be why Manlick et al. (2017b) did not observe strong snow depth effects in their smaller-scale occupancy models, but did using larger-scale species distribution models (Manlick et al. 2020). Similarly, Croose et al. (2019) found little evidence of spatial or temporal partitioning between martens and fishers in their 400 km² study area in the Upper Peninsula of Michigan, and concluded that other mechanisms of niche partitioning, not investigated in their study, were facilitating coexistence. These results stand in stark contrast to data from the northern Rocky Mountains (6400 km² study area), where the absence of martens was the best predictor of fisher occurrence and vice versa, after accounting for differential habitat selection (Fisher et al. 2013). Results of these two studies run counter to predictions based on range limit theory, where one would expect stronger biotic interactions at the southern range margin, but confirm likely issues caused by differences in scale. The scale of the study area used by Croose et al. (2019) is likely to have constrained their ability to detect environmental heterogeneity and elucidate mechanisms that permit sympatry within a larger landscape, whereas the study of Fisher et al. (2013) was conducted at a scale that incorporated substantial heterogeneity induced by gradients in topography and habitat.

Scale aside, the subcontinental variability in marten–fisher niche partitioning may also yield insights into the mechanisms permitting sympatry. In addition to snow depth, snow density, compaction, and surface hardness are important factors contributing to the effect of snowpack on species above the snow (Berteaux et al. 2017),

and potentially affecting marten–fisher spatial niche partitioning. For example, fur-harvest records have shown shifts in spatial dynamics between fishers and martens over the last 30 years that correspond to increased formation of ice crust on the snow surface, which in turn is due to increasing shifts in winter temperature (Suffice et al. 2020). Snow density is affected by wind, atmospheric temperature, temperature variability, and the frequency of phase transitions (e.g. rain-on-snow events). As all these are locally, regionally, and temporally variable (Berteaux et al. 2017), it is not surprising that the foot-loading disadvantage of fishers relative to martens is likewise highly variable.

SPATIAL HETEROGENEITY

Limitations imposed by habitat, climate, and hydrographic conditions all vary spatially, and the direct effects of these

on martens and fishers are manifest as spatial variability in each taxon's geographical range (Fig. 2). For martens and fishers, these abiotic conditions may be a key niche factor permitting coexistence or facilitating segregation. However, the limitations imposed by prey, predators, and competitors are also critical. Theoretical work on the role of spatial heterogeneity in facilitating sympatric species' coexistence suggests the interaction between geographically limiting abiotic resources (Grinnell 1917a,b, MacArthur & Levins 1964) and the shifting variability of those resources and intra- and interspecific competition (Fretwell 1969) can create conditions for stable sympatry (Chesson 2000, Amarasekare 2003). Amarasekare (2003) described two conditions where coexistence can arise in the absence of resource or temporal partitioning: spatially homogeneous and spatially heterogeneous competitive environments. Where conditions are spatially homogeneous, competition of coexisting species does not vary with biotic or abiotic

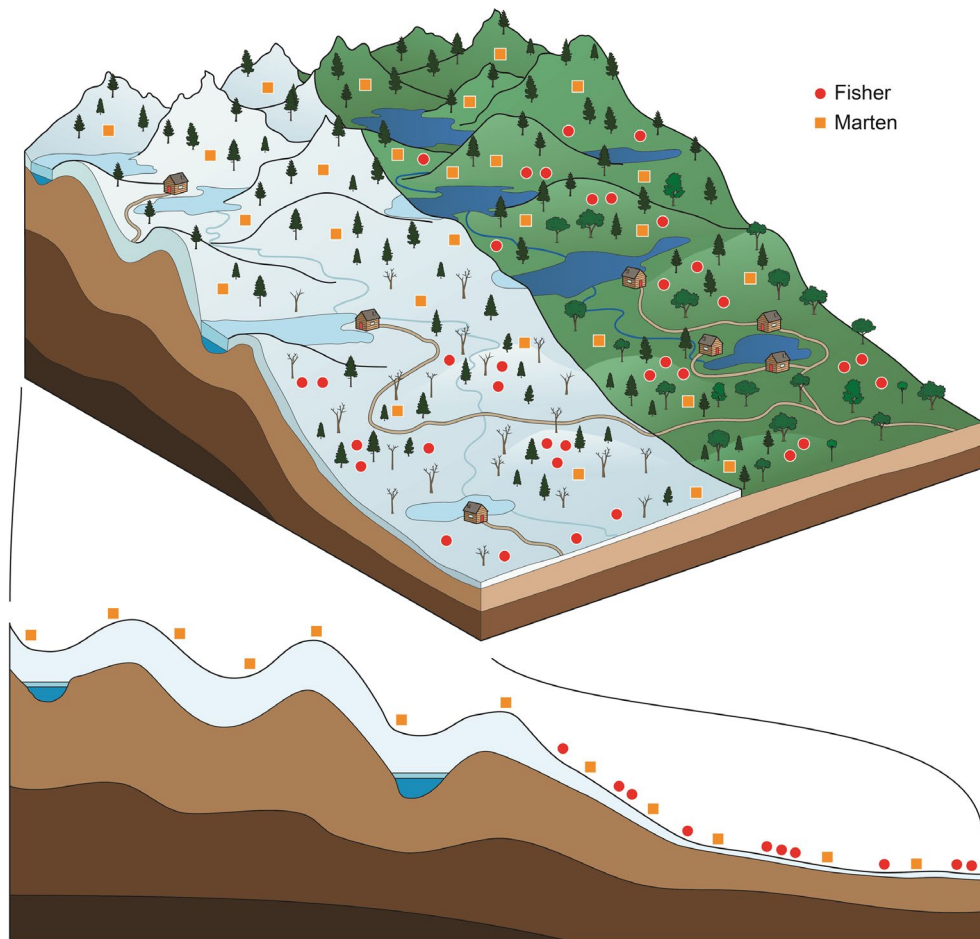


Fig. 2. Habitat heterogeneity promotes co-occurrence of martens *Martes* spp. and fishers *Pekania pennanti* throughout their geographical ranges. Complexity associated with topography and habitat allows the persistence of both species in a landscape. At lower elevations featuring more homogeneous forest types and increasing human presence, fishers are more common; at higher elevations, especially those featuring deeper snowpack, martens are more common.

conditions, whereas in spatially heterogeneous conditions, species' differential responses to these conditions create covariance between biotic or abiotic conditions and competition. This latter situation is more likely where life-history differences between species are minimal, as is found with martens and fishers (Fig. 2).

Within the geographical ranges of martens and fishers, heterogeneity results from variation in climate, topography, and elevation (which can interact with climate to create additional heterogeneity in rain or snowfall); these then influence spatial niche partitioning between fishers and martens. In the southern Sierra Nevada, where elevation and precipitation are highly variable, fishers and martens show a high degree of spatial niche partitioning, with little overlap in their distribution. Yet, at the southern boundary of this population, where variation in precipitation is reduced, the two taxa become sympatric with no apparent niche differentiation (Zielinski et al. 2017). In this area of sympatry, rugged topography and highly variable elevation may create fine-scale heterogeneity in climate or habitat that facilitates coexistence (Zielinski et al. 2017). In the Canadian Rocky Mountains where the two taxa segregate, landscape heterogeneity is likewise quite marked (Fisher et al. 2013). Conversely, in the Great Lakes region where elevation and topography are relatively uniform, Manlick et al. (2017b) did not find any evidence of spatial niche partitioning in a highly homogeneous landscape, resulting in complete niche overlap between fishers and martens. The authors concluded that in such a homogeneous landscape, competition was ultimately driving niche dynamics and that fisher presence was the primary factor limiting marten populations.

An alternative hypothesis is that snow and other abiotic factors may only be mediating, not limiting, influences. Implicated among these contrasting studies is the possibility of spatially mediated competition, wherein the outcomes of competition change across space as resources and limitations favour one taxon or the other. Spatially mediated competition can be inferred by current spatial segregation as an outcome of past competition rather than current behavioural choices. Fisher et al. (2013) inferred that spatially mediated competition resulted in martens dominating at some Rocky Mountain sites, and fishers at others. The competition outcome has less to do with individual dominance and interference competition, which has always been presumed to favour the larger fisher, and more to do with exploitation competition via heteromyopia (Murrell & Law 2003): higher local densities of subordinate martens exploit resources faster than dominant, but lower density, fishers. Here, marten–fisher segregation would necessarily be density-dependent: segregation would be observed in systems with high densities of each taxon, and not in systems with low densities. Both Manlick et al. (2017b)

and Croose et al. (2019) observed no segregation in Michigan and Wisconsin, where both taxa are reintroduced and martens are uncommon and occur at low densities. In the Canadian Rocky Mountains (Fisher et al. 2013) and Adirondack Mountains (Jensen & Humphries 2019), where segregation is starkly apparent, both taxa are relatively abundant, lending support for this inference.

Temporal partitioning and overlap

When competing species overlap spatially and in resource use, temporal activity can be modified to limit overlap and allow for coexistence (Kronfeld-Schor & Dayan 2003, Gerber et al. 2012). Consideration of temporal scale is important to identify and describe variations in temporal partitioning accurately (Wolkovich et al. 2014). A broad scale of temporal analysis is a 'season' (McCann et al. 2017), which informs how animals behave differentially as biotic and abiotic conditions shift with yearly environmental changes. Consecutively, smaller temporal scales include a 'day', which examines animal activity over 24-hour periods (Zalewski 2000); a 'bout', which covers continuous activity periods delineated by resting periods before and after (Patterson et al. 1999); and lastly a 'decision', which covers how animals forage and explore specific locations (McCann et al. 2017).

There are a number of mechanistic hypotheses to explain differences in temporal activity patterns of co-occurring species. The thermal conservation hypothesis postulates that carnivorans' activity tracks environmental conditions, such as excessive heat or cold, to allow them to expend the least amount of energy (Thompson & Colgan 1994), whereas the prey activity hypothesis asserts that predators are most active when their prey is active, to increase their foraging success (Zielinski et al. 1983, Martel & Dill 1995). Other proposed mechanisms include avoidance of the predator or dominant species by the prey or subordinate species (mortality risk hypothesis; Lima & Bednekoff 1999), avoiding resource competition from similar species (competition hypothesis; Kronfeld-Schor & Dayan 2003), and exploiting variation in light across lunar cycles to maximise foraging opportunities and reduce competition (Cozzi et al. 2012).

Common temporal segregation techniques used by subordinate species include avoiding shared habitats when a dominant species is present, altering daily circadian rhythms to avoid interaction, and exploiting seasonal patterns that may result in changes in competitive advantage between species (Bischof et al. 2014). Subordinate species may temporally avoid high-density areas or home range centres of species that can out-compete or directly harm them (Marneweck et al. 2019). This means that martens should use suboptimal habitat when fishers are active, and use

optimal habitat while fishers are resting (generally in the daytime). Another strategy involves altering circadian rhythms, which, in the case of fishers and martens, means that martens would become more diurnal. Lastly, seasonal shifts in resource use can facilitate niche differentiation if competitive advantage for resources shifts between species in accordance with seasonal changes in weather, as may be expected with martens' well-documented competitive advantage in soft deep snow conditions in winter.

Fishers and martens have shown temporal partitioning of resources, although this is not universal and is dependent on the scale of observation (McCann et al. 2017). At the 'day' scale, both fishers and martens are generally crepuscular (Zielinski et al. 1983, Arthur & Krohn 1991, Powell et al. 2003). In some instances, martens have been observed to become more diurnal in the presence of fishers (McCann et al. 2017, Croose et al. 2019), but this is not universal; some researchers have found the two taxa did not exhibit any temporal segregation (Frey et al. 2020). In intensely cold winter weather, martens have been observed to become more diurnal to lessen heat loss from their smaller bodies and avoid fisher activity (Thompson & Colgan 1994, McCann et al. 2017).

The most thoroughly studied region for temporal partitioning trends for fishers and martens is the Great Lakes region of North America. Here, sympatric marten and fisher populations in Wisconsin and the Upper Peninsula of Michigan did not exhibit spatiotemporal segregation at either daily or seasonal scales, and in fact, they showed a strong overlap in diel activity (Croose et al. 2019). Conversely, McCann et al. (2017) found that martens in northern Wisconsin reduced their activity at the day and bout scales when fishers were active, potentially to reduce their mortality risk. These contrasting results are likely to reflect different temporal scales of analysis (McCann et al. 2017). Mortality risk influenced marten activity at the broader scales (day and bout), but not at the finest scale (decision), showing that their daily temporal patterns are driven by broadscale avoidance of fishers. Mortality risk, competition, prey activity, and thermal conservation hypotheses are all supported when looking at spatiotemporal bouts of habitat patch use: martens are able to avoid peak fisher activity times while taking advantage of warmer daytime temperatures that result in more active prey.

In other regions, there is evidence for instances of temporal segregation of the two taxa. In southern Sierra Nevada, fisher and marten telemetry data suggest that martens rely on a combination of temporal and spatial avoidance to minimise agonistic interactions with fishers (Zielinski et al. 2017). Where fisher and marten home ranges overlap, there is simultaneous temporal avoidance of the overlap area by both taxa (Zielinski et al. 2017). In the boreal north-east, martens are more diurnal to

avoid extreme cold and to find increased amounts of prey, which naturally creates a distinct temporal niche that avoids fishers (Thompson & Colgan 1994). In the north-eastern USA, strong seasonal trends in prey and habitat use are observed for both fishers and martens (Jensen & Humphries 2019). Seasonal differences in snowpack, forest productivity, and the presence of an apex predator (the coyote) influenced when and how fishers and martens used the landscape to avoid dominant competitors while acquiring adequate forage. Multiple species interactions are likely to affect fisher and marten diurnal activity patterns, with the presence and intensity of segregation depending on landscape, disturbance, and community context (Frey et al. 2020).

A synthesis of niche partitioning and overlap

In contrast to the traditional view of highly specialised taxa, both martens and fishers appear broadly to be generalists; however, they also appear to be specialists in complexity, at least in space and resources. Indeed, both taxa are dietary generalists that readily adapt foraging to prey availability. Nevertheless, martens appear to select for small mammals (e.g. arvicolid rodents) throughout their range, while fishers preferentially use larger prey such as porcupines and snowshoe hares. Both taxa exhibit physiological costs, energetic costs (e.g. reduced nutritional condition), and fitness costs (e.g. lower reproduction) in the absence of preferred diet items, and prey limitation is likely to play a key role in trophic niche overlap and competitive interactions among martens and fishers (Carlson et al. 2014, Manlick et al. 2017b, Manlick & Pauli 2020). So, while there appears to be dietary overlap between these two competitors, there also is the opportunity for dietary divergence, when there is sufficient diversity of prey resources. Although widely considered habitat specialists, both martens and fishers similarly use a variety of the same types of forest habitat; in general, though, both taxa consistently use structurally complex forests, including closed-canopy areas, coarse woody debris, snags, and tree cavities that improve denning, foraging, thermoregulation, and predator avoidance (Buskirk & Powell 1994). Consequently, while both taxa use similar habitats, the structural complexity offered by their shared preferred habitats is likely to contribute to their coexistence via habitat partitioning (Fig. 2). Furthermore, the spatial heterogeneity offered by topographically diverse systems in both the Rocky Mountains and the Adirondack Mountains appears to provide another avenue by which martens and fishers can spatially partition to maintain sympatry.

Snow depth was identified long ago as an abiotic factor affecting marten and fisher partitioning (Raine 1983, Krohn et al. 1995), with differences in foot-loading and

consequent energy expenditure being implicated as potential mechanisms, reflecting the focus on morphology prevalent through the 20th Century. Snow continues to be a key factor: snow, and especially its interaction with elevation, appears to be an important driver of niche partitioning – martens select for deeper snow and access to the subnivium and small mammal prey in winter (Fig. 3). This suggests that for spatial segregation to occur, there needs to be a snow gradient present to maintain both taxa. However, there appears to be great variability in the magnitude of the effect, and even the direction of effects, for snow partitioning in different landscapes. This is insightful; for if snow depth and foot-loading were the main distinguishers, they would hold under most conditions. Instead, it appears that snowpack conditions, other abiotic factors, and biotic components of the system (e.g. productivity, prey abundance) are also important. Indeed, additional confounding effects such as human presence and disturbance, trapping pressure, and forest cover type may reinforce or alter the effects of snow and elevation, but have not been thoroughly investigated. Further, local winter weather conditions can alter these relationships with snow. A cold consistent winter with deep snowpack produces a high-quality subnivium, whereas a freeze–thaw cycle through the winter disrupts subnivium formation and stability (Thompson et al. 2021), while forming a surface crust that potentially reduces advantages to martens and conveys them to fishers (Fig. 3; Suffice et al. 2020).

Collectively, martens and fishers exhibit high degrees of diet and habitat overlap throughout their ranges. This

overlap in resource use (both prey and habitat) is likely to have the greatest fitness consequences for subordinate martens. Nevertheless, fine-scale habitat and prey partitioning, and especially partitioning along snow clines, are potential mechanisms by which these two taxa are able to coexist (Fig. 2). There also seems to be potential for martens to temporally adjust their activity to avoid encounters with fishers, although this is difficult to assess due to differences in timescales and approaches. A notable caveat is apparent in our review of past work: the patterns observed along each critical niche axes could be interpreted to support the hypothesis of abiotic heterogeneity, heteromyopic competition, or both. Keeping with the complexity of all ecological systems, it is likely that abiotic limitations and biotic interactions operate synergistically (or antagonistically) to create the observed distribution patterns.

It is interesting to consider similar relationships for other carnivorans, especially within the subfamily Guloninae. There are 11 recognised species within the subfamily but only two other species – stone marten *Martes foina* and pine marten *Martes martes* – exhibit notable overlap in their geographical ranges. Both species occur sympatrically in Central Europe, and where they co-occur, the stone marten is slightly larger (Wereszczuk & Zalewski 2015). Competitive overlap should, then, be more symmetric than observed for North American martens and fishers. Stone marten and pine marten diets overlap considerably, although the relative importance of food items appear to differ: stone martens consume more fruits and

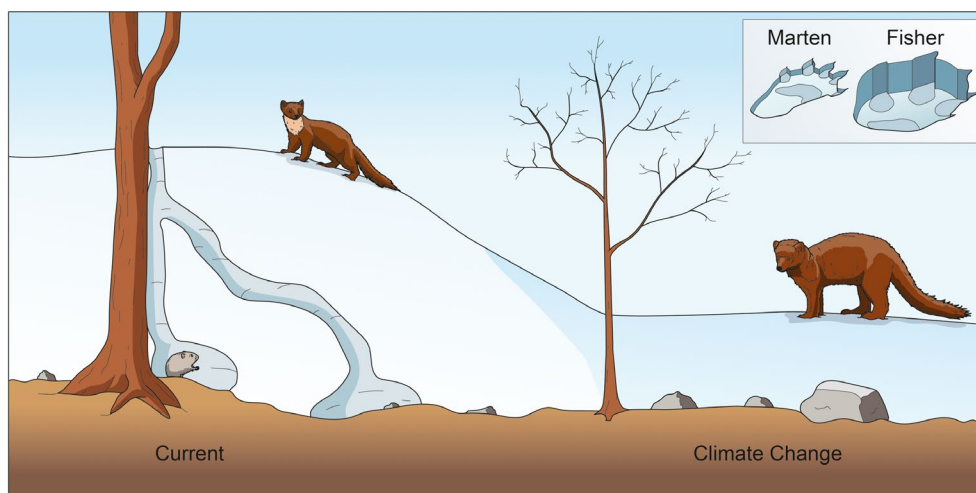


Fig. 3. Martens *Martes* spp. and fishers *Pekania pennanti* co-occur broadly in their geographical ranges. In areas of sympatry, however, deep powdery snow can create snow refugia for martens, for two reasons. First, martens are much lighter, possess lighter foot loads and therefore can traverse across the top of the snow rather than sinking in; fishers, on the contrary, are sufficiently heavy to sink into the snowpack due to their heavier foot loads and incur energetic costs in deep snow. Second, deep snow creates a subnivium, where martens can forage efficiently on important prey species (e.g. arvicolid rodents), whereas larger fishers are unable to exploit these prey. With warming climate generally creating shallower and denser snowpack for shorter durations, snow refugia are likely to become increasingly rare in many areas of marten and fisher sympatry.

insects, and pine martens consume more vertebrates (Postuszny et al. 2007). There is also evidence for temporal niche segregation, with both species being primarily nocturnal, but pine martens being more active during the day. Notably, stone and pine martens select different land-cover types and this appears to be the primary mechanism of partitioning: stone martens prefer developed areas, whereas pine martens prefer forests (Wereszczuk & Zalewski 2015). Stone martens now occur in North America: they escaped or were released from a fur farm in Wisconsin USA in the 1950s, and have been detected in a number of deciduous woodlots in south-eastern Wisconsin (Long 1995, Pauli 2013). The current range of stone martens does not coincide with that of native martens, but it does with that of fishers. How the introduction of exotic competitors will reshuffle observed interactions remains to be seen.

Future predictions with environmental change and directions for research and management

Few studies have investigated the effect of local density of either taxon on the form and the effect of competitive interactions between martens and fishers. For example, local density can alter exploitation competition where population abundance of the dominant competitor dictates availability of key prey species to the subordinate. Additionally, the frequency of interference interactions resulting in lethal and non-lethal outcomes is likely to be influenced by relative population densities. In this context, a focus on drivers that influence the density of the dominant competitor should provide a better understanding of observed patterns of sympatry or allopatry. Fisher–marten interactions are often considered to be unidirectional, with fishers, the dominant carnivoran, exerting strong top-down influence on martens. Less attention has been given to the possibility of two-way interactions between these taxa (e.g. Fisher et al. 2013) or age-structured interactions (Polis & Holt 1992). Future research, exploring not only the bidirectional nature of fisher–marten competition but also considering whether differences exist in the competitive relationships between fishers and each of the two marten species (i.e. fisher–American marten and fisher–Pacific marten), may reveal other mechanisms by which these closely aligned carnivorans persist in the landscape.

While previous studies have focused on fisher–marten interactions, few have examined the community and more complex interactions that may arise from higher and lower trophic levels. Thus, local densities of other competing carnivores, as well as bottom-up effects, need to be considered in future studies. As the importance of competitive interactions becomes better recognised, it seems increasingly

logical that the other species marten and fishers compete and interact with – including other mustelids, felids, and canids – will also drive the availability of resources. Other taxa are also affected by climate and topography, but many generalist carnivorans that are likely to compete with martens and fishers are now expanding their ranges into increasingly favourable climates (e.g. bobcats *Lynx rufus*, Peers et al. 2013; foxes *Vulpes vulpes*, coyotes). These changes will impact the abundance and availability of important prey species that in turn will affect these interactions within the carnivore community (Jensen & Humphries 2019).

Achieving a better understanding of these complex ecological factors is likely to require meta-analyses across diverse landscapes at large spatial scales and, as such, necessitates a shift in how research is undertaken. The complexity of the interactions combined with the large variation in ecological conditions among study areas brings into focus the need for both collaboration and standardisation among research groups. While many projects employ similar methodology (i.e. camera traps, hair snares, and global positioning system collars), there currently are no standards or guidelines for how to execute these methods in order to make data more comparable among studies. Without such standardisation, sharing or aggregating data into meaningful meta-analyses to address ecological questions at a broad scale is difficult. For example, while camera traps are routinely used by many researchers to collect species' detection data, protocols for the consistent collection of environmental data at camera sites (i.e. temperature, snow depth, and snow density) are almost non-existent: some researchers collect field measurements, while others rely on remotely sensed data. Even when using remotely sensed data, there is a lack of consistency in the covariates that are analysed and their sources, though standardisation would greatly increase comparability of results among studies. There is also little consistency in metadata standards for the cameras themselves, despite this having been recommended (Forrester et al. 2016). Employing such standards would ensure all necessary data are recorded and archived, in order to evaluate whether individual datasets can be used in meta-analyses. Lastly, with a growing awareness of the importance of spatially mediated competition (Amarasekare 2003, Murrell & Law 2003, Fisher et al. 2013), future research should focus on the interaction between local density and competitive interactions. This will require a significant shift from recent studies that have primarily relied on detection or non-detection data to more intensive methods used to estimate population density.

Fisher–marten interactions are sure to change in future, especially under current unprecedented environmental change. In particular, we predict that rapid ecological

change – especially from increasing anthropogenic habitat alteration and climate change – is likely to destabilise marten–fisher coexistence in areas of sympatry. The effects are likely to impact all three critical niche axes. Indeed, Manlick et al. (2020) recently found that marten–fisher co-occurrence increased with forest heterogeneity, but this was not the case in human-dominated landscapes, where heterogeneity took the form of forest fragmentation or human development. Similarly, a recent meta-analysis found that increased human disturbance decreased spatial niches for a diversity of mammalian species (Tucker et al. 2018). Although fishers and martens were not included in their analysis, effects are likely to be felt by the taxa, as increased disturbance is likely to minimise the potential for martens and fishers to partition space in the face of rapidly decreasing available habitat and space. Human disturbance has also led to increased nocturnality of carnivorans, thereby decreasing temporal (Gaynor et al. 2018) and dietary (Smith et al. 2018) niche partitioning, though these effects are different for martens than for larger carnivores (Frey et al. 2020). With further disturbance, the effects of shrinking temporal niche space are likely to continue to erode potential avenues for martens and fishers to segregate and co-occur. Both taxa consume human food subsidies in human-dominated landscapes (Manlick & Pauli 2020), resulting in trophic niche expansion and increased trophic niche overlap across the carnivore community. Martens generally exhibit less overlap with competitors (likely due to dietary shifts to avoid overlap), while fishers exhibit more overlap with competing carnivores in disturbed landscapes (Manlick & Pauli 2020). Moreover, in five sympatric populations of martens and fishers, human disturbance increased the dietary overlap experienced by martens but decreased the overlap experienced by fishers (Manlick & Pauli 2020). Thus, despite increasing diet overlap, marten–fisher competition could decrease in disturbed areas, because the dominant taxon (fisher) experiences less overlap, though competition with other carnivores is likely.

As climate change destabilises winters and the subnivium (Pauli et al. 2013, Zuckerberg & Pauli 2018, Zhu et al. 2019) and changes physical characteristics of snow (depth, density, and hardness; Boelman et al. 2019), heterogeneity in the competitive environment may shift (Amarasekare 2003). Indeed, increased snow compaction resulting from future warming winter temperatures is expected to facilitate fisher movement, and fisher and marten diet has been shown to overlap more in winter as fewer prey are available, so that increased snow compaction may adversely affect martens (Fig. 3). As mid-winter snowpack declines, the existence and stratifying impact of deep powdery snow and subnivium decrease. For martens, this would lead to a loss of exclusive foraging opportunities and stable thermal

refuges. As loss of the subnivium reduces the seasonal advantages of marten, their fitness and space use in normally snow-covered regions could see corresponding declines. Large prey species that experience increased natural mortality or vulnerability under harsh winter conditions (e.g. white-tailed deer) would be less available to fishers, which would decrease overall prey availability and the ability to stratify prey consumption. Indeed, it appears that under projected climate change, fishers and martens will experience distributional and numerical declines and increased isolation at their southern range boundaries, and a number of currently vulnerable populations – especially of martens – will be driven to extirpation (Lawler et al. 2012).

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